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Vulnerability of Juvenile Clams to Predation by Shore Crabs

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Abstract

Predation, especially by crabs, is a common source of mortality for natural and farmed populations of intertidal clams. Consumption of juvenile “seed clams” forces aquaculturists to try to exclude predators and/or raise juveniles in hatcheries until they can reach a size refuge. We ran a variety of lab experiments assessing vulnerabilities of juvenile clams to small, common shore crabs (*Hemigrapsus* spp.). Crabs <1 cm width can consume hardshell Manila clams larger than those normally used for “seed”, and can readily crush even larger softshell *Mya* clams. We suggest that using netting to prevent consumption by shore crabs is not practical given that smaller individuals can fit through mesh openings. Raising seed in hatcheries until they are 10-15 mm will provide a size refuge from shore crabs, but not larger cancrid crabs. Farming on beaches with little habitat (e.g., cobbles) for shore crabs can likely reduce juvenile clam mortality. A better understanding of predation threats to commercially important clams is critical, especially as the invasion of the green crab *Carcinus* to Washington shorelines further threatens survival of juvenile clams.

1. Introduction

Aquaculture is an increasingly important contributor to food production and the global economy, with the worldwide farming of shellfish increasing by 650% in the past 30 years (Saurel, Ferreira, Cheney, Suhrbier, Dewey, Davis, Cordell, 2014). While some aspects of shellfish farms raise ecological and aesthetic concerns (Bendell, 2015; Munroe, Kraeuter, Beal, Chew, Luckenbach, Peterson, 2015), culturing bivalves (oysters, mussels, and clams) can provide ecosystem services as well as a valuable protein source. These services include reducing water turbidity and excess nitrogen (Higgins, Stephenson, Brown, 2010), sequestering carbon in shells, and even reducing wave energy that erodes shorelines (Peterson, Grabowski, Powers, 2003).

A substantial challenge to the success of both farmed and natural populations of shellfish is reducing loss to predators. Diverse consumers such as seastars, carnivorous snails (whelks and moonsnails), crabs, birds (shorebirds and diving ducks), and fishes (bony fishes and rays) can all reduce densities of adult clams (Beal, 2006; Bendell, 2015; Beukema, Dekker, Philippart, 2010; Munroe, McKinley, 2007; Myers, Baum, Shepherd, Powers, Peterson, 2007). Recently settled (<1 mm) clams of various species are also vulnerable to mortality from a range of predators including crangonid shrimp, juvenile crabs including hermit crabs, grapsids, and portunids, nereid polychaetes, and perhaps even nematodes (Beukema, Dekker, 2005; 2014; Hunt, Scheibling, 1997; Olafsson, 1989; Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002; Whitton, Jenkins, Richardson, Hiddink, 2012; Williams, 1980). Slightly larger clams (2-5 mm) can be eaten by other predators including nemertean worms, numerous crab species, and

mummichog and other fishes (Beal, Vencile, 2001; Hunt, Mullineaux, 2002; Peterson, Summerson, Huber, 1995; Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002).

Large losses of clams at shellfish farms to predators, especially crabs, leads to expensive mitigation efforts to increase clam survival (Peterson, Summerson, Huber, 1995). “Seed clams” (usually 1-15 mm) have higher survival following outplanting when they are protected from predators by plastic nets (reviewed by Munroe, Kraeuter, Beal, Chew, Luckenbach, Peterson, 2015) or by coarse substrate such as gravel added to the sediment surface (Glaspie, Seitz, Ogburn, Dungan, Hines, 2018; Peterson, Summerson, Huber, 1995; Ruesink, Freshley, Herrold, Trimble, Patten, 2014). Coarser substrates may give clams surfaces to attach to for stability (Becker, Barringer, Marelli, 2008) or make it harder for predators to dig (Arnold, 1984; Liu, Wang, Lu, Hu, Su, Liu, Zhu, 2019). Ironically, in some cases adding coarser substrate may encourage residence of small crabs, which can consume seed clams (Smith, Langdon, 1998). However, netting and sediment amendment will not increase survival if a key mortality source is small predators that are undeterred by the large mesh of most anti-predator netting.

The Manila clam, *Ruditapes philippinarum* (Adams & Reeve, 1850) (also known as *Venerupis philippinarum*, *Venerupis japonica* and *Tapes japonica*), is an important fisheries species in the Caribbean, Mediterranean, North Atlantic Ocean and North Pacific Ocean. In 2014, global production was 4,000,000 tons (Cultured Aquatic Species Information Programme 2005: http://www.fao.org/fishery/culturedspecies/Ruditapes_philippinarum/en). Manilas were introduced to the US west coast in the late 1930s and are now an important farmed species in Washington State (Smith, Langdon, 1998). Another introduced species that is less broadly farmed in Washington is the softshell clam *Mya arenaria* Linnaeus, 1758, which is an

economically critical shellfish species in the northeast US (Glaspie, Seitz, Ogburn, Dungan, Hines, 2018). For Manilas, as many as 100,000 larvae per m^2 may settle into natural sediment (Tezuka, Kamimura, Hamaguchi, Saito, Iwano, Egashira, Fukuda, Tawaratsumida, Nagamoto, Nakagawa, 2012) but <1% survive to harvestable size (40 mm in length; e.g., Williams, 1980). This very high post-settlement mortality could stem from abiotic factors such as salinity or temperature variation, or biotic factors such as predation and competition for resources (Dethier, Ruesink, Berry, Sprenger, 2012; Hunt, Scheibling, 1997; Williams, 1980).

As part of a larger study on sources of mortality to juvenile clams on Washington shorelines, we investigated the vulnerability of juvenile clams to crab predation, and how this is affected by clam size and species. Here we focus on the potential role of shore crabs, *Hemigrapsus nudus* (Dana, 1851) and *H. oregonensis* (Dana, 1851). These small (< 4 cm width) crabs are abundant on shorelines from Alaska to the Gulf of California, inhabiting numerous habitat types (mud to bedrock) but especially soft-sediment shorelines where cobbles or debris give them protection at low tide (Harger, 1972; Kozloff, 1993; Low, 1970). The two species are largely sympatric although *H. oregonensis* tends to prefer somewhat more wave-protected shores (Harger, 1972). Unlike other decapods such as cancrid crabs or invasive green crabs (*Carcinus maenas*) that are known consumers of shellfish, Quayle (1988) dismissed *Hemigrapsus* as important predators on shellfish; he noted that these species are commonly found under clusters of oysters but that “they are scavengers and do no harm to oysters” (p. 93). Other authors have considered them to be herbivorous or omnivorous (Knudsen, 1964; Yamada, Boulding, 1998).

While *Hemigrapsus* spp. are not usually considered to be significant intertidal predators, we hypothesized that they could contribute to high field mortality of newly settled clam spat and

juveniles. We were particularly interested in when clams reach size refuges from these predators. If small crabs that are not excluded by shellfish farm netting can consume seed clams, then seed clam sizes may need to be increased to reduce field mortality.

2. Methods

2.1 Field data on predator densities

Work reported elsewhere (Dethier, Kobelt, Yiu, Wentzel, Ruesink, 2019) at study beaches around Washington State quantified abundances of large (> 5 cm) cancrid crabs, but mesh size of the Fukui traps used was too large (12 mm) to retain smaller predators such as shore crabs. We counted shore crabs in quadrats along 50 m horizontal transects in the mid-shore (+1 m above Mean Lower Low Water (MLLW)), but found that this method also did not effectively quantify these mobile predators; at low tide they tend to cluster under cobbles or debris (e.g. logs, netting) that were not necessarily found along the transect. We thus present data from other studies showing the ranges of abundances of shore crabs on Washington beaches. These data (Dethier, Schoch, 2005) come from monitoring surveys of over 30 sites and up to 15 years. In each case, site-date values are counts of crabs averaged over ten 0.25 m^2 quadrats along horizontal transects at either MLLW or +1 m MLLW.

2.2 Lab experiments with crabs consuming clams

Experiments were conducted in indoor sea tables with running seawater (at 10.5-12.3^o C) at the Friday Harbor Laboratories (FHL), Washington (48^o 32’ 45” N 123^o 00’ 45” W) during 2017. We worked with juvenile clams of two commercially important species: *Ruditapes philippinarum* (Manila clams) that were obtained from Taylor Shellfish at 1 or 2 mm shell length

or field-collected at larger size; and softshell clams *Mya arenaria* that were collected at various field sites. All clams were kept in sea tables while being fed Shellfish Diet 1800 (Instant Algae®). Shore crabs *Hemigrapsus nudus* and *H. oregonensis* were collected from under intertidal cobbles on the FHL beach. For all individuals used in experiments we measured both carapace width and dactyl length (inner surface) of the larger claw. Yamada and Boulding (1998) show that female crabs have smaller claws; we did not track sex as we assumed that the key parameter in ability to consume clams was claw size regardless of sex. Crabs were fed ulvoid algae if kept in lab for more than several days, but were always starved for 24 hours before experiments. Each individual crab was only used in one experiment.

We tested the abilities and preferences of *Hemigrapsus* spp. of different sizes to consume clams of different sizes. Feeding trials were run by placing individual crabs in small (ca. 10x10x10 cm) lidded plastic containers with mesh sides to allow water flow. Pilot studies quantifying predation rates with or without sediment in the containers showed no consistent differences, so experiments were run without sediment to improve the consistency of data collected. To determine how large a clam could be consumed by crabs, a single measured (length) clam was placed in a container with a crab. After 24 hours, the clam was recorded as intact or crushed and consumed, and the crab was measured and released. Most experiments were run with small Manila clams, but some parallel trials were run with juvenile *Mya arenaria*.

To determine relative predation rates, individual crabs were given 10-20 small measured Manila clams, either all one size (to quantify consumption rates) or of a range of sizes (to quantify preferences). Numbers and sizes consumed were quantified after 24 hours.

3. Results

3.1 Predator densities at field sites

In quadrats at eight sand-pebble beach sites (Dethier, Kobelt, Yiu, Wentzel, Ruesink, 2019), *Hemigrapsus* spp. were sparse (overall average of less than one per 0.1 m^2 quadrat) and tended to be very small (average size of 5 mm) individuals that could hide effectively along the transect in clam holes or under pebbles. More and larger (up to 3 cm) individuals were seen when cobbles or debris were overturned at almost any intertidal elevation. Other beaches in the state (see Methods) had densities of *H. oregonensis* ranging from 4-40/m^2 in the mid shore (at ~+1 m, N = 82 site-date combinations) and 0.4 to 20 in the low shore (MLLW, N = 186 site-dates). Highest densities were found where cobbles provided shelter on sand or gravel beaches. *H. nudus* is more common higher on the shore than at either of these transect elevations (Dethier, pers. obs.) and tends to be more abundant at higher-energy sites (Harger, 1972; Kozloff, 1993). Yamada and Boulding (1996) reported densities of *Hemigrapsus* spp. up to 300/m^2 on optimal gravel-cobble beaches. Low (1970) found that densities of both species were very low (ca. 0.1/m^2) on bedrock shores and on plain sand and mud beaches with little 3D structure, but as high as 500/m^2 on beaches with loose rocks on the surface. The amount of cover, especially from cobbles, was the best predictor of abundance of both crab species. Diverse vertebrates prey on them, including raccoons, gulls, a variety of fishes, and many diving ducks, so significant populations are only found where they have refuges during both low and high tides (Low 1970).

163 3.2 Lab experiments with crabs

164 Our feeding observations showed minimal differences in predation rates or preferences
165 between *Hemigrapsus nudus* and *H. oregonensis*, so we pooled results from these two taxa.
166 Both crab species ranged in sizes of carapace width from approx. 5 to 25 mm and dactyl length
167 from 0.5 to 7.7 mm. The tight correlation ($r^2 = 0.88$, N = 66) between carapace and dactyl sizes
168 suggests that at least in our sampled mixed-gender and mixed-species population, there was
169 not a substantial difference among sexes or species in relative claw sizes (Suppl. Fig. 1). Here we
170 report results by dactyl length, assumed as the more relevant parameter for ability to break a
171 clam shell.

172 Both shore crab species showed high individual variance in behavior in terms of how many
173 small (2 mm) clams they ate in a given 24 hour period. Crabs of every size tested ate from 0 to
174 10 (all) clams per day, with no discernable pattern to these differences (N = 126 trials; Suppl.
175 Fig. 2). We thus focus our analyses on how big a clam *could* be eaten by a particular size crab,
176 and on relative rates of predation as crab and clam sizes were varied. We found that even the
177 smallest *Hemigrapsus* tested (~1 cm carapace width, with ~1 mm dactyls) could crush 2 mm
178 Manila clams. When offered the thinner-shelled *Mya* clams, small crabs could crush a much
179 larger individual compared to Manila clams (Figure 1); a 12 mm (carapace width) crab with a 2.5
180 mm dactyl could crush a *Mya* almost its size (11 mm shell length). Larger Manila individuals (ca.
181 10 mm) could only be crushed by the larger (~25 mm carapace) shore crabs.

182 Because we had few juvenile *Mya* available for experiments, predation rate experiments
183 with shore crabs were run only with Manila clams. Small crabs (dactyl < 4 mm) readily ate small
184 (<5 mm) clams, sometimes consuming all 10 offered within 24 hours (Fig. 2). The data from

185 medium-sized crabs (dactyl 4-6 mm; carapace 15-20 mm) show a pattern of the crabs eating
186 fewer large clams than medium or small ones in the same period of time. Large crabs readily
187 ate all sizes of clams including the larger individuals (Fig. 2).

188 When medium to large (mean dactyl length 6.8 mm: carapace width ~20mm) shore
189 crabs were offered a choice of 5 individuals of each of the 3 size classes of clams, they showed
190 no preferential consumption for any size (Suppl. Fig. 3), eating ca. half of all the clams
191 regardless of size.

192 **4. Discussion**

193 Crabs inhabiting the intertidal zone on Washington state shorelines (e.g., *Hemigrapsus*
194 spp.) or foraging there at high tide (cancrids; also majids, *Telmessus*: pers. obs.) likely constitute
195 significant sources of mortality for clams, as has been shown in numerous other systems (see
196 Introduction, also Boulding, 1984). Unfortunately, it is difficult to precisely quantify abundances
197 of such mobile predators. Other investigators have tried to quantify densities via snorkeling at
198 high tide (Grosholz, Ruiz, Dean, Shirley, Maron, Connors, 2000) or benthic trawling (Glaspie,
199 Seitz, Ogburn, Dungan, Hines, 2018). Crab abundances can be very patchy, e.g. due to local
200 hypoxia (Altieri, 2008), or the presence of refuges from their predators, e.g. from gulls (Beal,
201 2006). The *Hemigrapsus* shore crabs we worked with are broadly present on Washington
202 shorelines except at the most wave-exposed beaches, and can be present in hundreds per m^2 in
203 areas where cobbles or debris provide low-tide refuges (Low, 1970). Thus, their predatory
204 impact on juvenile clams could be substantial.

We found that in the lab, even very small *Hemigrapsus* spp. can crush and consume not only juvenile softshell clams (*Mya*) but hardshell Manilas. Clams <5 mm were consumed by even the smallest shore crabs tested (carapace width 5-10 mm). Adult shore crabs (carapace >20 mm) readily ate 8 mm clams, even hardshell Manilas. Some crabs tended to eat fewer large clams than smaller ones in the same period of time; this could result either from longer handling times (not measured), or satiation when eating the larger prey. Crabs were very individualistic in terms of feeding rates; under identical conditions (starved, then offered clams for 24 hours in lab), some ate nothing while others consumed all the clams available.

As in other studies, consumption by crabs clearly varies not only with clam size but with shell morphology (see also Boulding 1984), with the thinner-shelled *Mya* more vulnerable to crushing. When clam shells are weakened by acidified porewater conditions, (Glaspie, Longmire, Seitz, 2017; Green, Waldbusser, Reilly, Emerson, O'Donnell, 2009), this vulnerability to shell-crushing predators increases. Some experiments have also shown that crab feeding behavior can be directly affected by pH (Glaspie, Longmire, Seitz, 2017), complicating our ability to predict the effects of this increasingly relevant abiotic stressor.

Our data thus contribute to the literature on the ability of clams to reach size refuges from their predators. In our system, Manila clams, despite their hard shells, do not reach a size refuge from the very common intertidal shore crabs until they are >12 mm. Although we did not run experiments with adult clams, it is likely that there is no size refuge for Manilas from the cancrid crabs that were present at most of our sites (Boulding, 1984; Boulding, LaBarbera, 1986; Dethier, Kobelt, Yiu, Wentzel, Ruesink, 2019; Yamada, Boulding, 1996; 1998). Small (20 mm) *Cancer oregonensis*, for example, can consume oysters over 30 mm length (Yamada,

Metcalf, Baldwin, 1993). Survival of farmed Manila clams to harvestable size thus must rely on netting to exclude large crabs, except in the few places where crabs are naturally rare. Eliminating predation on seed clams by shore crabs is likely impossible using netting, since mesh size would have to be <1 cm to keep out the small crabs that are capable of consuming 2 mm clam seed. A viable alternative may be raising seed in hatcheries until they at least 10-15 mm, achieving a size refuge from shore crabs. This relatively large 'safe' size may be adequate for various thick-shelled clams (Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002) but may need to be larger (>20 mm) when dense blue crabs are present (Peterson, Summerson, Huber, 1995). 'Safe' seed size for softshell clams is hard to calculate because they are so readily crushed, or even peeled through their siphonal gape (Boulding, 1984). For shore crabs, farming on beaches lacking the cobble or debris that provide crab habitat may help reduce juvenile clam mortality.

Predation by crabs thus is a multifaceted problem for the valuable shellfish aquaculture industry, especially when the crabs are diverse in their sizes and behaviors, as is true on the tide flats in Washington. The continued invasion of the green crab *Carcinus maenas* into the inside waters of Washington (Grason, McDonald, Adams, Litle, Apple, Pleus, 2018; Yamada, Thomson, Gillespie, Norgard, 2017) will further exacerbate the challenge of clam losses to crab predators.

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375

FIGURE CAPTIONS

Figure 1. Relative sizes of crabs (*Hemigrapsus* spp.) and clams in trials where crabs were able to consume the clams offered. N = 33 trials with Manila clams, N = 20 trials with *Mya*. R^2 values of linear regression for each clam species: *Mya* 0.20, Manila 0.46.

Figure 2. Predation rates by crabs on Manila clams of varying sizes. Crab Dactyl sizes: Small ≤ 4 mm; Medium = 4.1 to 6.0; Large = 6.1 to 8.0 mm. Bars are mean and one s.e. of N trials; replicate N's per bar (left to right) = 130, 0, 0, 41, 12, 8, 19, 14, 18. No trials were run (ND = no data) attempting to feed medium or large clam categories to small crabs.

Figure 1.

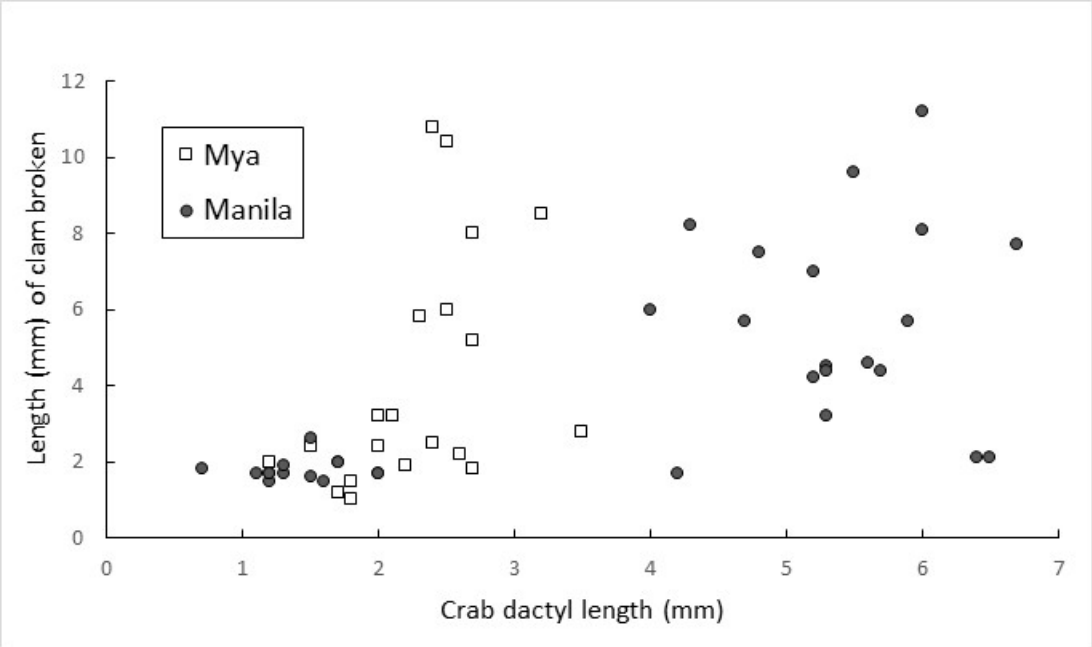
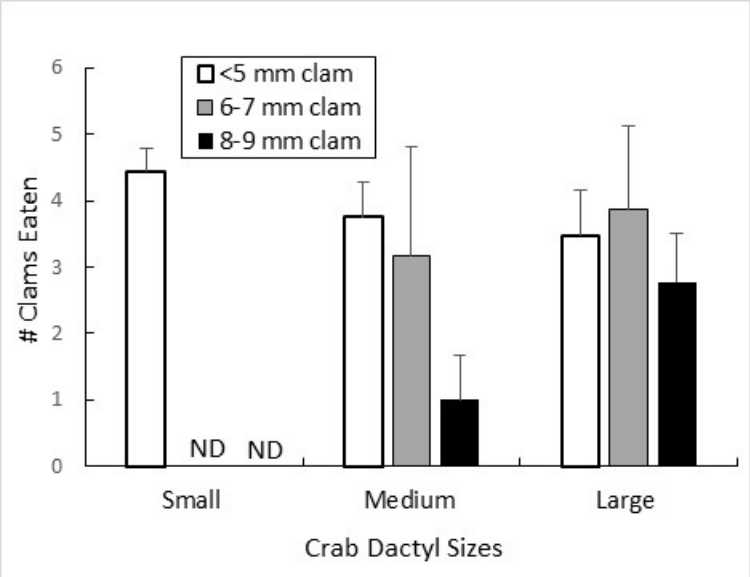
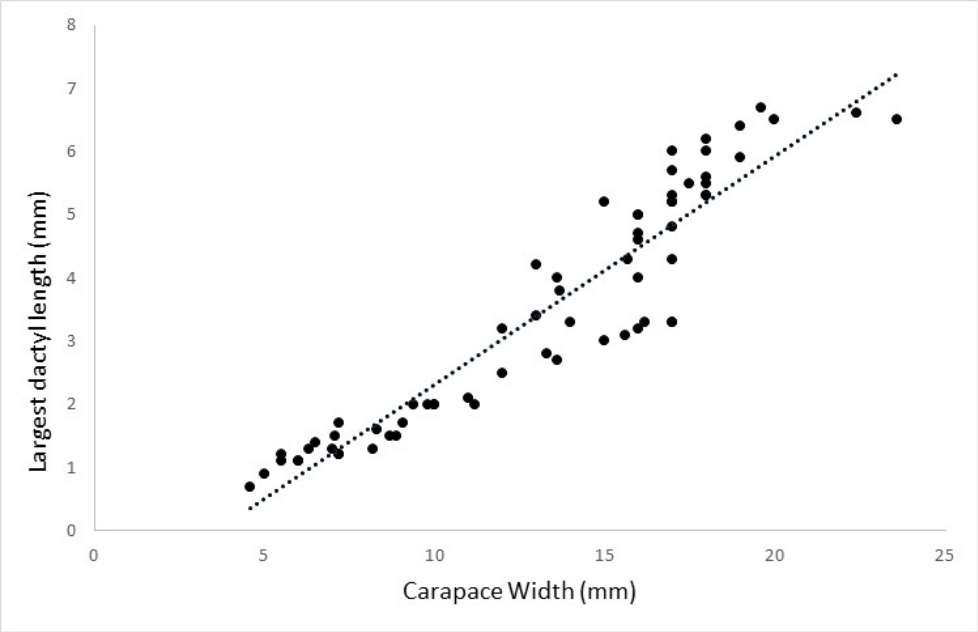

Mya
Manila
Length (mm) of clam broken
Crab dactyl length (mm)
0
2
4
6
8
10
12
0
1
2
3
4
5
6
7

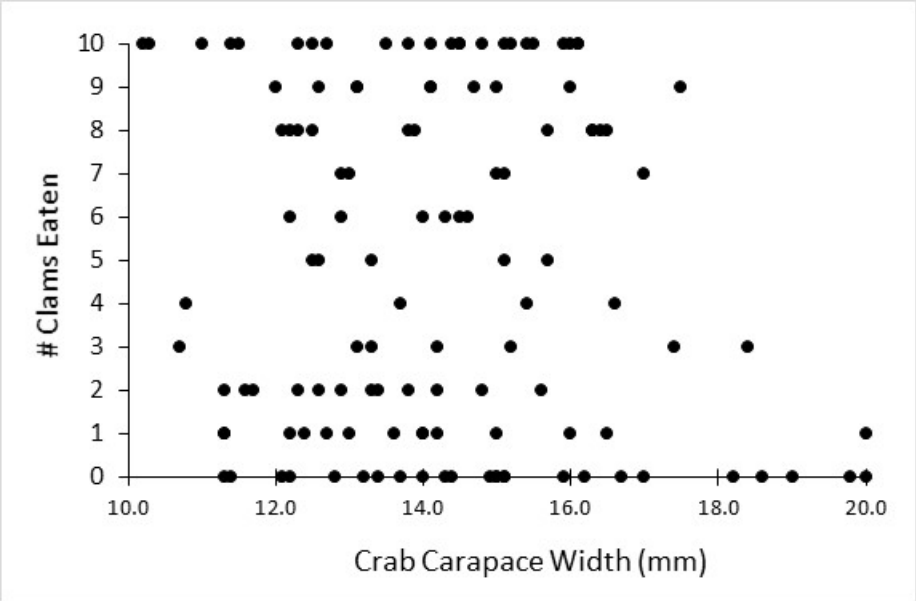
Figure 2.


<5 mm clam
6-7 mm clam
8-9 mm clam
Clams Eaten
0
1
2
3
4
5
6
ND
ND
Small
Medium
Large
Crab Dactyl Sizes

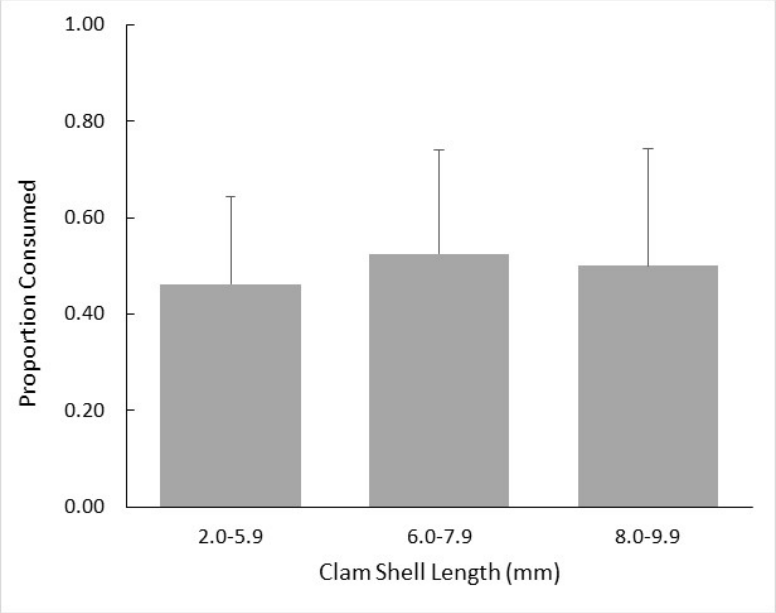
Dethier et al. **SUPPLEMENTAL FIGURES**



Supplemental Figure 1. Correlation between carapace size and dactyl length for *Hemigrapsus oregonensis*. N = 66 crabs, $r^2 = 0.88$



Supplemental Figure 2. Numbers of small (2 mm) clams eaten out of 10 offered to different sizes of *Hemigrapsus* spp. over 24 hours. N = 126 trials, each point is a separate individual crab.



Supplemental Figure 3. Mean (one s.d.) proportion of clams consumed by shore crabs when offered a choice of 5 clams of each size class. N=16 trials (separate crabs).